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Effects of Short-term Soil Conditioning by Cheatgrass and Western Wheatgrass

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ABSTRACT The exotic grass *Bromus tectorum* (cheatgrass) is a ubiquitous invader in the western USA. Cheatgrass is a proficient competitor, frequently displacing native plants, forming monotypic stands and reducing biodiversity in ecosystems it invades. Our experiment tested whether short-term soil modification by cheatgrass and a predominant native grass, *Pascopyrum smithii* (western wheatgrass), affected subsequent growth of both species. We compared productivity of cheatgrass and western wheatgrass by harvesting aboveground biomass of plants grown in either cheatgrass- or western wheatgrass-conditioned soils over two simulated growing seasons. Results indicated that cheatgrass soils do not inhibit the productivity of the native grass, but do facilitate further growth of cheatgrass. Cheatgrass may alter soil characteristics, allowing it to invade other plant communities, but cheatgrass invaded soil did not inhibit growth of the native species studied here. This suggests that restoration with native species after control of cheatgrass may be possible.

KEY WORDS *Bromus tectorum*, invasive species, *Pascopyrum smithii*, plant-soil interactions, semi-arid steppe, shortgrass prairie.

Soil conditioning by plant species can alter soil properties, from changes in physical properties such as pH, to changes in the microbial community (Klironomos 2002). Many studies have indicated that soil conditioning by exotic plant species may be an important mechanism allowing them to invade and dominate native ecosystems (Callaway and Aschehoug 2000, Corbin and D'Antonio 2004, Wolfe and Klironomos 2005, Jordan et al. 2008). Depending on the specific ecosystem and species, these changes may happen as quickly as two growing seasons (Bezemer et al. 2006, Perkins and Nowak 2013) or may take years to accumulate and manifest (Belnap et al. 2005).

In the western USA, one of the most damaging invasive plant species is *Bromus tectorum* (cheatgrass), an annual grass native to the Mediterranean (Valliant 2007, USDA 2011*a*). Understanding the characteristics that allow cheatgrass to become abundant in many plant communities is an ongoing area of research. Currently, cheatgrass is the most ubiquitous exotic grass in the steppe of the Intermountain West (Mack 1981). Cheatgrass has induced changes in fire frequency and attributes in areas of the Great Basin (Pimentel et al. 2000). Fire is a vital factor in assuring the survival of cheatgrass in semi-arid shrub-steppe (Knapp 1996). Cheatgrass benefits from fire because it is an early successional species; in post-burn sites, cheatgrass is able to occupy the limited resource niche that most natives are unable to fill (Knapp 1996). In the foothills and grasslands east of the Rocky Mountains where fires were historically common, however, increasing cheatgrass abundance has not been associated with decreasing fire-return intervals (Veblen et al. 2000, Bromberg et al. 2011, Beals et al. 2014).

Although frequent fire reinforces invasion of cheatgrass, multiple mechanisms, including the effect of cheatgrass on soil properties (e.g., Perkins and Nowak 2013) also can support invasion. The most important nutrient to study is the one most limiting to plants in the communities it invades—usually nitrogen (LeBauer and Treseder 2008). As documented for several invasive plants, cheatgrass biomass gain is greater than native species when exposed to increased levels of nitrogen (Vasquez et al. 2008, Witwicki et al. 2012). Cheatgrass showed biomass gains at every increase in nitrogen level, whereas a Colorado native (Blue grama [*Bouteloua gracilis*]) stopped responding at an early level of increase (Lowe et al. 2003). Cheatgrass has been shown to alter soil biota, reducing the number of nematode and fungi taxa within the first few years of invasion (Belnap et al. 2005). In controlled studies, other invasive grasses, including the related *B. erectus*, altered soil properties in even shorter times (Bezemer et al. 2006). One way that cheatgrass may alter soil properties is through litter quality, as cheatgrass litter has significantly greater C:N and Lignin:N ratios compared to most native species (Evans et al. 2001). Although numerous studies have looked at the impacts of cheatgrass on soil characteristics, relatively fewer have examined the effects these changes have on growth of cheatgrass and natives, and how quickly cheatgrass can affect soil properties (but see Perkins et al. 2011, Perkins and Nowak 2012, 2013). In our study, we examined the effects of short-term soil conditioning by cheatgrass on the growth of cheatgrass and a native grass. We hypothesized that cheatgrass may condition soils in a way that enhances its own production while simultaneously inhibiting the growth of native species, specifically the native prairie grass, western wheatgrass [*Pascopyrum smithii*].

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STUDY AREA

Soils for this experiment were collected from a semi-arid shortgrass prairie at an elevation of 1,798 m approximately 15 km northwest of Boulder, Colorado, USA (N 4440750, E 474436). The site received an average of 475 mm of precipitation per year and had an average temperature of 10.5° C (WRCC 2012). Soils at the field site have been classified as well drained, colluvial, sandy loams (USDA 2001). Cheatgrass was likely introduced to this site in the early 1900s when the area was heavily grazed by cattle (Prevéy and Seastedt 2014).

METHODS

Study Species

Cheatgrass is commonly a winter annual, although under dry fall conditions cheatgrass also may germinate in the spring (Finnerty et al. 1962). Several adaptations give cheatgrass competitive advantages over native species. Its carbohydrate metabolism enables cheatgrass to grow at comparatively low temperatures and thus gain an early advantage over native grasses, which may still be in a state of dormancy (Chatterton 1994). Cheatgrass has fibrous, fine, heavily-divided roots, and these roots are capable of penetrating up to 152 cm in depth, but most root mass is present in the first 20 cm of soil (Hulbert 1955). Cheatgrass displays a large degree of plasticity in its morphology and phenology. For instance, in arid conditions it may only produce one culm with a single spikelet; in a more fertile environment it may produce hundreds of culms (Upadhyaya et al. 1986).

Western wheatgrass is a perennial grass native to the Great Plains of the USA (USDA 2011*b*). Western wheatgrass is one of the most common cool-season grass species in the western Great Plains, and has certain adaptations to help its survival and competitive ability. Western wheatgrass has large quantities of long, branching rhizomes that help it survive periods of acute water stress (Wasser and Shoemaker 1982). These rhizomes exist most commonly 1.25 to 5 cm below the soil surface, although roots may penetrate a depth of up to two meters. However, in less fertile soils such as those in eastern Colorado, this depth is generally limited to less than 1.5 m (Coupland and Johnson 1965). Western wheatgrass regenerates by belowground axillary buds and by seed (Ott and Hartnett 2015), but western wheatgrass stands are known to develop relatively slowly from seeds (Sedivec et al. 2011). This may be an important disadvantage in comparison to fast-growing invasive species.

Soil Collection

On 9 May 2011, we collected soils for our greenhouse experiment from beneath a stand of the non-native cheatgrass [C-soil] and from beneath a stand of the native western wheatgrass [W-soil]. Each soil collection site had >95% cover of the target species. We collected soils to a maximum depth of 20 cm because we wanted to use soil that was directly impacted by the plant growth above. On the C-soil, small quantities (less than 1% cover) of tumble mustard [*Sisymbrium altissimum*], prickly lettuce [*Lactuca serriola*], and ragweed [*Ambrosia psilostachya* var. *coronopifolia*] also were present. Cheatgrass-dominated sites had no bare ground and an abundance of litter. The W-soil had small quantities (less than 2% cover) of blue grama, Canada bluegrass [*Poa compressa*], white sagebrush [*Artemisia ludoviciana*] and Northern Idaho biscuitroot [*Lomatium orientale*]. Wheatgrass dominated soils had significant bare ground. We removed large rocks, litter, and roots from soils and then transported them to the greenhouse.

We measured abiotic and biotic properties of the soils collected for our experiment and properties of 18 additional soil samples from below monocultures of cheatgrass and western wheatgrass. We used these measurements to assess differences between cheatgrass-dominated and western wheatgrass-dominated soils and to evaluate whether soil nitrogen varied over the growing season. We collected soil samples below the 10 stands of cheatgrass or western wheatgrass in September 2011, and April, June and August 2012. The first two sampling locations were the same as those of the soils used for the greenhouse experiment. All samples were located within 800 m of the initial sampling location, and we collected soils from areas that had either 95% cheatgrass or western wheatgrass cover. To account for landscape level variation, we paired sites of either cheatgrass or western wheatgrass within 20 m of each other, and these paired sites were greater than 30 m from other paired sites. We collected each soil sample from a depth of 0–10 cm, homogenized it, and separated it into sub-samples for different analyses. For each soil sample we measured texture, % organic content, inorganic nitrogen, C/N ratios and soil biomass C and N.

We determined soil texture using mechanical analysis (Kilmer and Alexander 1949). To measure available inorganic nitrogen, wet soil subsamples were extracted with 2M KCl to leach inorganic nitrogen. We estimated the amount of NO_3 and whatever traces of NO_2 might be present, and NH_4 in KCl extractions using a Lachat QuikChem 8500 Flow injection analyzer [Hach Company, Loveland, CO, USA]. To measure C/N ratios, subsamples were dried, ground and analyzed for %C and %N with a Carlo ER-BA CHN analyzer. Results from soil carbon and nitrogen analyses are expanded from Concilio et al. (2015). We measured soil biomass C and N on soil samples from April and June 2012, using the chloroform fumigation-direct extraction method (Brookes et al. 1985); approximately 10 g of soil was used for each fumigated and non-fumigated soil sample. We extracted soil samples with 0.5M K_2SO_4. The amount of C and N in K_2SO_4 extracts were measured on a TOC-V CPN total organic carbon analyzer and a TNM-1 total nitrogen measuring unit.

In August 2012, we collected aboveground biomass and litter biomass from each sampling site. Standing aboveground biomass was collected from a 0.1 m^2 area centered above each soil sample and clipped at ground level. Litter biomass was collected from the same area. Biomass samples were dried in an oven at 60° C for three days and then weighed.

Greenhouse Experiment

The soil-conditioning experiment consisted of two subsequent experiments. Experiment 1 tested how cheatgrass and western wheatgrass grew in their own and the other's soil, while experiment 2 tested if one season of soil conditioning by a species would affect subsequent growth of either species (Fig. 1). We placed the collected soil in 2-L pots on 15 May 2011 and mixed it with perlite to increase oxygen content and prevent clumping (~85% field soil, ~15% perlite). We filled 48 pots with either C-soil (24 pots) or W-soil (24 pots). We then sowed 6 cheatgrass seeds or 6 western wheatgrass seeds in 12 pots of each soil type in a 2 × 2 (seed × soil) factorial design with 12 replicates of each treatment combination (Fig. 1, Experiment 1). We collected cheatgrass seeds from the site the previous year, and western wheatgrass seeds were purchased from a local native plant nursery (Arkansas Valley Seed Inc, Denver, CO). We acknowledge that there could be differences between locally adapted and commercial seed sources, however, seed yield of western wheatgrass at our site was low, and so we could not collect enough seeds for this experiment. In addition, purchasing seeds of invasive species such as cheatgrass is difficult.

We grew plants in pots from 15 May 2011 to 15 July 2011 for experiment 1. Each experiment lasted ~60 days. Every three days, each pot received 300 ml of water. This watering regime ensured soils were frequently, but not continuously, moist or waterlogged. About once per month, we randomized all of the pots on the table to account for variation in microclimate and light resulting from position on bench. Temperatures in the greenhouse over the two experiments averaged 21° C, with lows of ~12° C and highs of ~32° C. Because the soils from the field were not sterilized, occasionally seeds of species we did not plant sprouted in pots. We removed unwanted seedlings as they were found. Additionally, naturally occurring cheatgrass seeds germinated in pots. In pots with more than six individuals, excess individuals were trimmed to the ground, as pulling would have disturbed individuals we wished to retain. Pots that did not have more than two individuals germinate in the first two weeks were re-seeded to result in 6 individuals per pot. Newly planted individuals grew to similar sizes as older seedlings by the end of the experiment.

Experiment 1 ended on 29 July 2011. We cut all aboveground biomass at ground level from each pot, dried the bio-

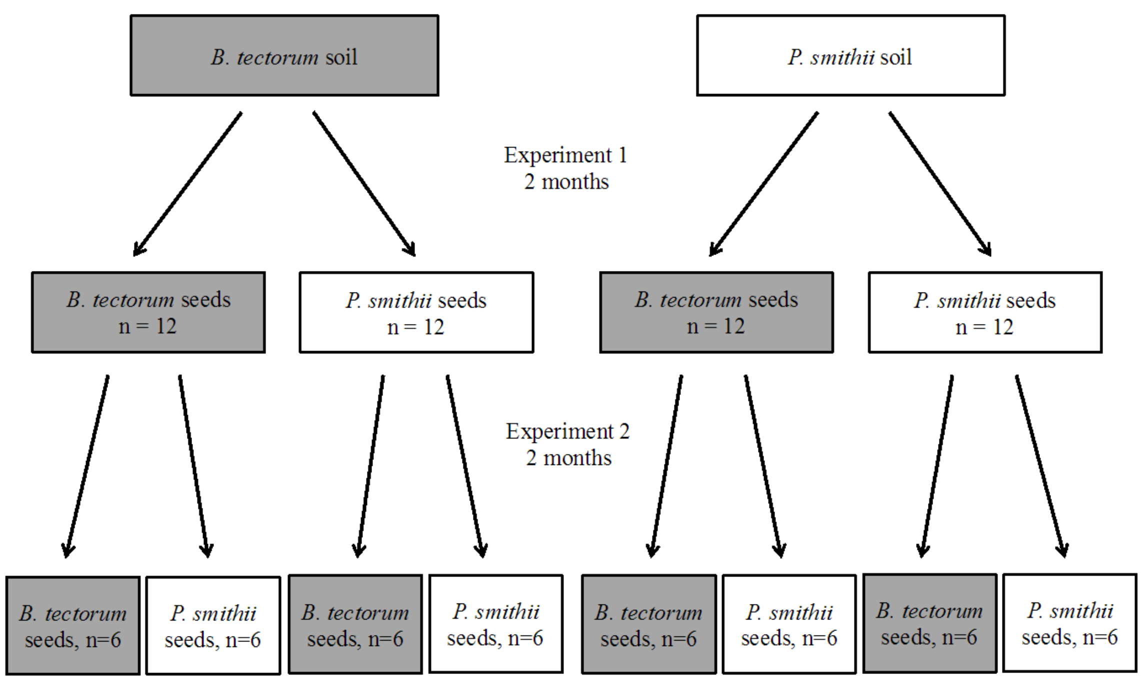

Figure 1. Diagram of greenhouse experimental design. The letter "n" indicates the number of pots in the greenhouse with the indicated species of seed. Field collected cheatgrass and western wheatgrass soil was placed in 48 pots planted with either cheatgrass or western wheatgrass seeds in experiment 1, and then replanted with either cheatgrass or western wheatgrass seeds in experiment 2.

mass at 60° C for three days, and weighed it to the nearest 0.01 g. Total biomass in each pot was divided by the number of individuals in each pot to calculate average biomass per seedling. We removed the roots of plants in every pot. To help ensure that there were no survivors from experiment 1, pots were checked every day for six days to remove any individuals that resprouted.

Experiment 2 tested how one season of cheatgrass or western wheatgrass growth influenced subsequent growth of both species. For instance, we wanted to evaluate whether western wheatgrass-dominated soil that had experienced one generation of cheatgrass growth was more beneficial to further cheatgrass growth than to western wheatgrass. To test this, we used potted soils from the original four treatment groups to create a 2 × 2 × 2 factorial design, with two levels of field soils type (C-soil and W-soil), two levels of plant growth from experiment 1 (cheatgrass and western wheatgrass), and two levels of plant growth for experiment 2 (cheatgrass and western wheatgrass). This resulted in 8 different treatments with 6 replicates per treatment (see Fig. 1, Experiment 2). On 2 August 2011, we planted six seeds of either species in each pot. By 27 August, the majority of pots still had moist soil by the next scheduled watering period. From this point onward, we watered plants every four days, though the reduction in watering frequency did not create any visible signs of water stress. On 30 October 2011, we ended experiment 2 and quantified the number of survivors in each pot, and measured aboveground biomass.

Statistical Analyses

We compared soil texture, % organic matter, % carbon, % nitrogen, C:N ratios, soil biomass C and N, aboveground biomass, and litter biomass with blocked analysis of variance (ANOVA) tests. We considered soils collected from paired cheatgrass/western wheatgrass sites blocks in our analyses. Percent carbon, % nitrogen, and litter biomass did not fit assumptions of normality and were square-root transformed before analysis. Before analysis of inorganic nitrogen samples, we removed nitrogen values that were greater than 3 standard deviations from the mean so samples with anomalously high nitrogen did now skew results. This led to the removal of five samples from analysis. To handle the resulting unbalanced data, we used linear mixed-effects models to compare NH_4, NO_3 and total nitrogen between cheatgrass-dominated and western wheatgrass-dominated soils. We considered soil type and sampling date fixed effects, whereas block was considered a random effect in the models. We log transformed NH_4, NO_3 and total nitrogen values before analysis to better fit assumptions of normality.

We analyzed the effect of soil type on aboveground biomass (g) of cheatgrass and western wheatgrass (e.g., greenhouse experiment) with two-way ANOVAs for experiment 1 and 3-way ANOVAs for experiment 2. Prior to analysis, we square-root transformed all biomass data to meet assumptions of normality; results were considered significant at $\alpha < 0.05$. We adjusted P-values for interactions from the 3-way ANOVAs for multiple unplanned comparisons. We conducted all statistical analyses using LME4 and PHIA (e.g., 'testFactors') packages in program R (R Development Core Team 2012, De Rosario-Martinez 2015).

RESULTS

Soils collected from the field had similar texture and % organic matter (Table 1). However, cheatgrass soils had significantly higher % C, % N, soil biomass C and N, and NO_3 than western wheatgrass soils ($P < 0.05$; Table 1, Fig. 3). Western wheatgrass and cheatgrass soils had similar aboveground biomass in August 2012, but cheatgrass soil had twice as much litter biomass as western wheatgrass soil.

After experiment 1, aboveground biomass of both species was almost three times greater in C-soil than in W-soil ($F_{1, 44} = 24.90$, $P < 0.01$; Fig. 2a) and cheatgrass grew twice as much aboveground biomass as western wheatgrass in both soil types ($F_{1, 44} = 11.84$, $P < 0.01$; Fig. 2*a*). Cheatgrass grown in C-soil had the highest biomass of the four treatments and biomass of western wheatgrass grown in its own soil had the least biomass (Fig. 2a). After the experiment 2, soil type again strongly affected biomass ($F_{1, 40} = 29.08$, $P < 0.01$; Fig. 2b). The species of plant grown in experiment 1 (cheatgrass or western wheatgrass) did not significantly influence plant biomass in experiment 2 ($F_{1, 40} = 0.26$, $P = 0.86$; Fig. 2b). Cheatgrass still had the greatest biomass across all eight soil by seedling treatments ($F_{1, 40} = 161.79$, $P < 0.01$; Fig. 2b). There were no significant interactions between soil and seed species in either experiment 1 or 2 (all $P > 0.06$).

DISCUSSION

Our results indicated that soil type and plant species were significant factors in determining productivity of cheatgrass and western wheatgrass. Cheatgrass grown in its own soil had the greatest productivity, and grew significantly better on its own soil than soil previously occupied by western wheatgrass. Western wheatgrass grown in its own soil had the lowest productivity, while western wheatgrass grown on cheatgrass soil produced more biomass than when grown on its own soil. It is important to note that cheatgrass is an annual plant, while western wheatgrass is a perennial, and cheatgrass may have grown larger at a faster rate because of these different life history strategies.

The results from experiment 1 do not support the hypothesis that soils dominated by cheatgrass decrease the production of native western wheatgrass. Cheatgrass did not condition soils in a way that inhibited growth, but actually benefited productivity of western wheatgrass. In contrast to our hypothesis, western wheatgrass grew larger in soils from

Table 1. Measurements of soil variables ± standard error for cheatgrass and western wheatgrass soils. Values significant at the 0.05 level are denoted with an asterisk. For soil variables that were measured multiple times over the growing season, the values shown are averaged over all measurements. NH_4, NO_3, and total nitrogen were analyzed with linear mixed models, and all other variables were analyzed with blocked ANOVAs. Soil carbon and nitrogen results previously reported in Concilio et al. (2015).

Measurement	Cheatgrass soil	Wheatgrass soil	*P*
% Sand	74.07 ± 0.39	73.16 ± 0.31	0.59
% Silt	15.43 ± 0.30	17.30 ± 0.24	0.18
% Clay	10.50 ± 0.26	9.56 ± 0.28	0.35
% Organic matter	10.14 ± 0.28	9.20 ± 0.21	0.35
% Carbon*	3.74 ± 0.34	2.65 ± 0.15	<0.01
% Nitrogen*	0.32 ± 0.03	0.22 ± 0.01	<0.01
C:N ratio	11.62 ± 0.21	11.85 ± 0.14	0.32
Biomass C (mg/g soil)*	0.58 ± 0.07	0.39 ± 0.05	0.02
Biomass N (mg/g soil)*	0.07 ± 0.01	0.04 ± 0.01	0.04
Biomass C:N	9.74 ± 0.72	10.19 ± 0.89	0.82
NH_4/g soil	7.09 ± 1.36	5.66 ± 0.96	0.14
NO_3/g soil*	9.52 ± 1.66	4.90 ± 1.38	<0.01
Total inorganic N*	16.61 ± 3.02	10.56 ± 2.33	<0.01
Aboveground biomass (g)	11.41 ± 1.69	12.70 ± 1.96	0.64
Litter biomass (g)*	36.77 ± 6.94	19.17 ± 2.40	<0.01

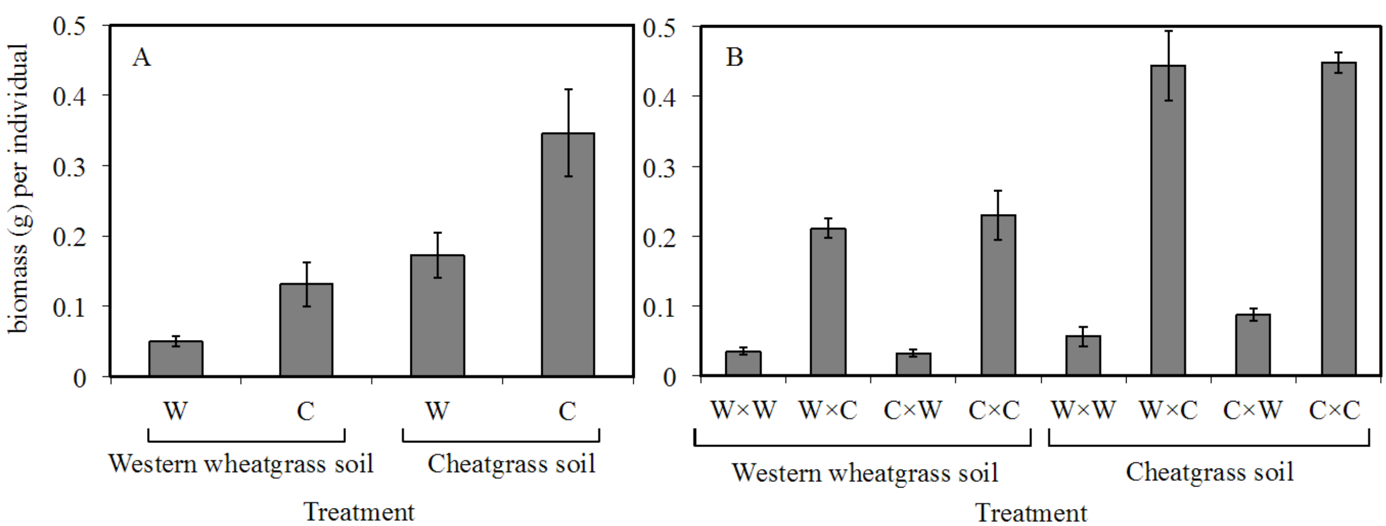

Figure 2. (A) Aboveground biomass harvested after experiment 1. For treatment labels, W indicates pots with western wheatgrass seeds, and C indicated pots with cheatgrass seeds. (B) Aboveground biomass in pots after experiment 2. The first letter of the treatment label denotes the species of seed (W = western wheatgrass and C = cheatgrass) planted in pots in experiment 1, and the second letter denotes the species of seed planted in experiment 2.

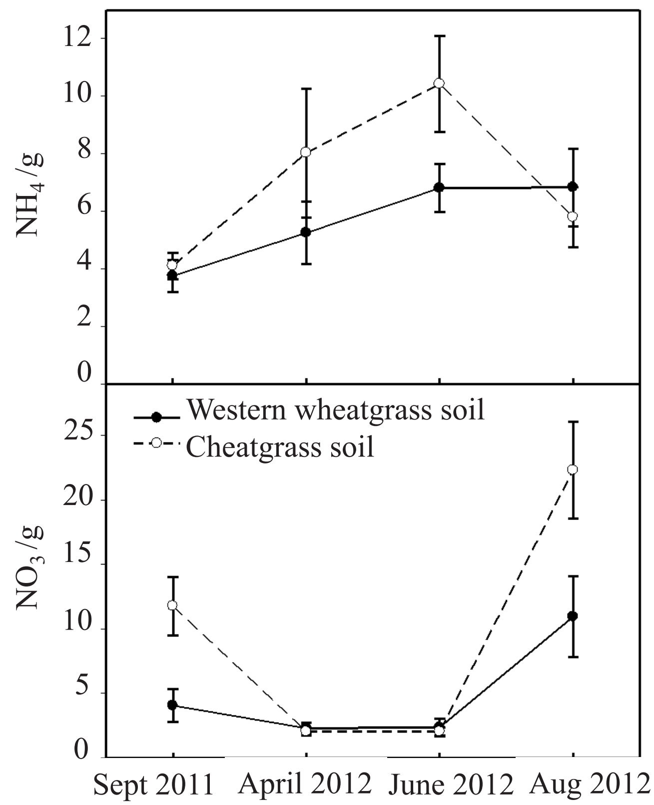

Figure 3. µg NH_4 per gram of soil (top panel), and µg NO_3 per gram of soil (bottom panel), in western wheatgrass and cheatgrass soils over the four sampling dates, ± standard error. Information presented here is expanded from Concilio et al. (2015).

cheatgrass-dominated stands than in its own soil. Findings from our greenhouse experiment contrast with results from other studies that show negative or neutral effects of invasive-modified soils on native species (Callaway et al. 2004, Perkins and Nowak 2012). In our study, western wheatgrass consistently had the lowest productivity in its own soils. Our results support the idea that many native species experience negative plant-soil feedbacks in their own soils, possibly due to higher abundance of native pathogens reducing growth, whereas a new soil environment may provide an escape from these pathogens (Bever 1994, Klironomos 2002). Alternatively, the higher N found in soils beneath cheatgrass stands could increase subsequent growth of western wheatgrass, or both changes could have positively affected western wheatgrass growth.

There are two main possibilities regarding how an increase in soil fertility allows cheatgrass to out-compete its neighbors. As cheatgrass becomes more productive on soil which it has conditioned, its heightened response allows it to out-compete grasses that are on the edge of its conditioned soil, and so the cheatgrass-conditioned soil, along with cheatgrass, spreads. The ability of invasive plants to take advantage of more nutrient-rich environments compared to natives has been observed multiple times (Vitousek 1994, Lowe et al. 2003, Weltzin et al 2003; but see Funk and Vitousek 2007). The other possibility is that cheatgrass is able to form relationships with soil biota that thrive on productive soils, relationships that western wheatgrass (the dominant species of many nitrogen-limited grasslands) does not possess. Previous studies have shown that cheatgrass can alter the microbial community in its soils (Belnap et al. 2005, Perkins and Nowak 2013), and these alterations may benefit cheatgrass more than other species. Other successful invasive plants have been shown to create beneficial relationships with soil microbes (van der Putten et al. 2013).

Our study does not provide evidence that cheatgrass or western wheatgrass can modify soil conditions over a single growing season. Results from experiment 2 showed that neither species had significantly different productivity in soils that had experienced one season of growth by the same species. Although cheatgrass was more productive on soils from cheatgrass -dominated stands, this does not necessarily show that soils were more fertile because of cheatgrass. The soils that cheatgrass dominated at the field site may have been more fertile prior to cheatgrass invasion, although several studies indicate cheatgrass can increase nitrogen stocks in soil (Ehrenfeld 2003, Blank 2008, Stark and Norton 2015).

Our research supports results of previous studies emphasizing the importance of soil properties to cheatgrass growth. This should direct research efforts to more closely examine the interaction between cheatgrass and soil biota, nutrient cycling, and soil structure. Future research using more than two generations of an invasive plant species may help determine the timeframe over which invasive species can significantly modify soils. Additionally, measuring soil characteristics along a known gradient of invasion times could indicate the time period necessary for soil alterations by invasive species.

MANAGEMENT IMPLICATIONS

Our study provides important insights for land managers on possible mechanisms promoting cheatgrass persistence in the western Great Plains. Soil modification by cheatgrass may promote invasion and persistence of the species. Examining soil properties of regions susceptible to cheatgrass invasion could help land managers prepare and prioritize their efforts to minimize the spread and introduction of cheatgrass. Additionally, the positive response of native grass grown in cheatgrass-modified soil suggests that restoration with native species may be possible if cheatgrass is removed from areas it has invaded.

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